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THE EFFECTS OF MORPHINE ON THE DISCRIMINATION OF SUBJECT-
PRODUCED AND EXPERIMENTER-IMPOSED DURATIONS

by

Ryan D. Ward

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Psychology

Approved:

UTAH STATE UNIVERSITY
Logan, Utah

2005

ABSTRACT

The Effects of Morphine on the Discrimination of Subject-

Produced and Experimenter-Imposed Durations

by

Ryan D. Ward, Master of Science

Utah State University, 2005

Major Professor: Dr. Amy L. Odum

Department: Psychology

Experiments on the effects of drugs on behavior maintained by temporal-discrimination procedures have led to discrepant results. Recent experiments suggest that the effects of drugs may differ depending on whether the subject is timing some aspect of its own behavior or some other stimulus. The present experiment used a multiple-schedule procedure composed of a subject-produced and experimenter-imposed component. In the subject-produced component, pigeons categorized the duration of their most recently emitted interresponse time. In the experimenter-imposed component, pigeons categorized the duration of a key light. Morphine generally produced underestimation of time during the subject-produced component, a result in agreement with other recent experiments. Morphine had no systematic effects on accuracy during the experimenter-imposed component. These results are discussed in terms of procedural interactions and a morphine-induced disruption of stimulus control.

(54 pages)

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Ryan D. Ward

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INTRODUCTION

Psychologists have been interested in the perception of time since the early days of the field. One reason for this interest is the fact that distorted perception of duration is a symptom of several psychological disorders. Research on the timing of durations has revealed that the processes underlying accurate timing of events by humans and nonhumans are similar. Because of the similarities between the process of timing in humans and nonhumans, studying this phenomenon in animals may be beneficial.

One important area of research is the effects of drugs on the perception of time. In an influential experiment, Maricq and Church (1983) assessed the effects of methamphetamine on temporal discrimination in rats. Methamphetamine produced overestimation of the duration of the sample. Maricq and Church interpreted this overestimation as resulting from an increase in the speed of an internal clock. Based on evidence from this study and other experiments, Meck (1996) proposed the neuropharmacological model of timing. In this influential model, Meck proposed that increased dopamine levels affect timing by increasing the speed of an internal clock, which in turn leads to overestimation of time. Although many experiments have reported overestimation of time as a result of administration of dopamine agonists (e.g., Eckerman, Segbafia, Manning, & Breese, 1987; Frederick & Allen, 1996; Maricq, Roberts, & Church, 1981), many others have not (e.g., Frederick & Allen; Knealing & Schaal, 2002; Odum, 2002; Odum, Lieving, & Schaal, 2002). There are serious discrepancies in the timing literature that have not been resolved.

Recently, Chiang et al. (2000) suggested that the discrepant results could be due in part to different procedures used across experiments. In two experiments, they

showed that different timing procedures did in fact produce discrepant results. Their explanation for these results was that different mechanisms of timing may be tested with different procedures. Specifically, they suggested that administration of drugs may have different results on behavior depending on whether the subject is timing some aspect of its own behavior or some external event.

Relatively few studies have investigated the timing of what will hereafter be referred to as subject-produced durations. To test the hypothesis of Chiang et al. (2000), it is important to study this type of timing. Shimp (1981) used a procedure in which pigeons produced interresponse times (IRTs) of two duration categories: short and long. Following production of sample IRTs pigeons categorized the duration emitted as either short or long. Shimp found that the pigeons were able to emit the required IRTs and correctly categorize them. Using this procedure, Odum and Ward (2004) found that morphine produced underestimation of time. In previous research, Odum and Schaal (2000) reported that morphine produced underestimation of the duration of experimenter-imposed stimuli. Although the results of Odum and Ward were similar to these results, it is important to note that their experiment only assessed the effects of morphine on the discrimination of subject-produced behavior and is therefore not a direct comparison.

The present research incorporated both experimenter-imposed and subject-produced timing tasks within the same session. Specifically, the procedure consisted of a multiple schedule in which the first component was a temporal-discrimination procedure based on the one used by Shimp (1981), in which pigeons produce and discriminate IRTs of short or long duration. The second, experimenter-imposed,

component presented pigeons with short or long sample durations that were yoked from the IRT durations in the first component. The pigeons then categorized the durations as short or long. The effects of a range of doses of morphine were then assessed. Because the present experiment utilized a procedure in which both types of timing were assessed within subjects, it provided a stringent test of Chiang and colleagues' (2000) hypothesis regarding the effects of pharmacological manipulations on both subject-produced and experimenter-imposed timing.

LITERATURE REVIEW

The study of the perception of time is important for a number of reasons and has been of interest for a long time in psychology. An organism can be said to be timing if “our clock is a better predictor of its behavior than any other stimulus we can identify” (Killeen, Fetterman, & Bizo, 1997, p. 80). Accurate processing of relevant temporal information is critical for the conduct of many daily activities. In addition, the importance of the study of timing can be seen in the finding that distorted perception of temporal duration is symptomatic of a number of human disorders, including Parkinson’s disease (e.g., Malapani, Deweer, & Gibbon, 2002), schizophrenia (e.g., Rammsayer, 1990), and attention-deficit/hyperactivity disorder (e.g., Levin et al., 1996).

Experimental psychologists have extensively studied timing in nonhumans. Studying the process of timing in nonhumans is advantageous for several reasons. First, the genetic and behavioral history of subjects can be precisely controlled. This additional control facilitates the goal of this type of research: to isolate physiological mechanisms responsible for accurate timing. In addition, a laboratory environment provides the ability to manipulate experimental variables and conditions with a precise degree of control not generally found in research with human subjects. Research has shown that the process of timing in animals and humans is similar (e.g., Rakitin et al., 1998). Therefore, studying the processes underlying timing of durations in animals may help us uncover and describe some of the mechanisms that may be used in human timing. Using a variety of procedures, many researchers have attempted to identify and uncover the mechanisms responsible for timing in animals.

In an important and influential experiment, Maricq and Church (1983) examined the performance of rats on a psychophysical timing task. Left lever responses were reinforced with food if the duration of a signal (blackout) was 2.5 s, and right lever responses were reinforced if the duration of the signal was 6.3 s. The experimenters inserted several probe trials with signals of varying durations to which responses were never reinforced. To obtain an indication of the perception of time they plotted right (i.e., long) responses as a function of signal duration. Figure 1 shows an example of such a function.

When the percentage of long choices is plotted as a function of time, the function is generally sigmoid in form and increases from left (short sample durations) to right (longer sample durations). This result indicates accurate perception of the sample durations. In Maricq and Church (1983), in the absence of amphetamine, the functions indicated accurate control of behavior by the temporal stimuli.

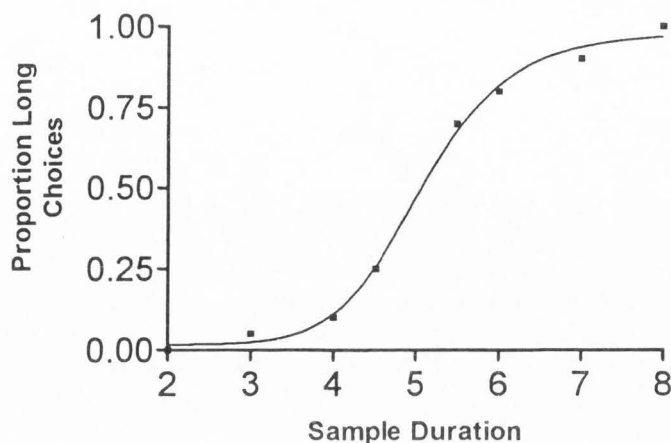


Figure 1. Hypothetical data showing proportion long choices as a function of sample duration.

Methamphetamine flattened the psychophysical function and shifted it leftward. Maricq and Church (1983) interpreted this shift to reflect an increase in the speed of an internal clock. Haloperidol, on the other hand, flattened the psychophysical function and shifted it to the right, interpreted as a decrease in the speed of the internal clock. Finally, a combination of methamphetamine and haloperidol led to a function similar to the saline control function.

Discrepancies in the Timing Literature

Based on this evidence and evidence from other experiments, Meck (1996) proposed a neuropharmacological model of timing, which states that the speed of an internal clock is controlled by dopamine and acetylcholine. The more dopamine present, the faster the clock ticks. With more dopamine present and a faster clock, the organism is expected to overestimate the amount of time that has passed. This overestimation is indicated by an immediate leftward shift in the psychophysical function. A decrease in dopamine levels is predicted to have the opposite effect, with a rightward shift in the psychophysical function, indicating underestimation of time.

As part of the support for his model, Meck (1996) cited experiments in which the dopamine agonist amphetamine increased rates of responding early in the initial portion of fixed-interval (FI) schedules of reinforcement. In an FI schedule, a reinforcer is delivered for the first response after a specified amount of time. The typical response pattern during the FI is a pause following the delivery of a reinforcer, followed by a steadily accelerating response rate through the terminal peck (Ferster & Skinner, 1957). Fixed-interval schedules and many variations of them have been used

extensively to study the effects of drugs on timing because the behavior maintained by them is especially sensitive to the effects of pharmacological agents.

In an early experiment, Dews (1958) trained pigeons on an FI 15-min schedule and then exposed them to amphetamine. During the absence of drug the pattern of responding was typical of responding on FI schedules. Response rates were low during the first part of the interval and increased during the second part of the interval until the reinforcer. In the presence of amphetamine, however, response rates increased in the early part of the interval and decreased somewhat in the later part of the interval. Dews did not interpret this finding to reflect an increase in the speed of an internal clock. In fact, he cautioned against interpreting the results as evidence of disruption of timing, stating: "None of these interpretations adds anything to the understanding of a drug effect, and they may interfere with recognition of a relatively simple and consistent effect of the drug" (Dews, p. 146).

Odum et al. (2002) investigated the effects of *d*-amphetamine on the timing of experimenter-imposed stimuli using a procedure based on one first described by Reynolds and Catania (1962). Pigeons were presented with a sample and then given the opportunity to peck a key for 30 s. The sample was presented for either 5 or 30 s. Following the presentation of the sample, the center key was lit with either blue or green light. Pecks to the blue key were reinforced intermittently if the sample duration had been 5 s and pecks to the green key were reinforced intermittently if the sample duration had been 30 s. Trials in which intermediate sample durations were presented were also inserted. During these trials, pecks to the center key had no programmed consequence.

When response rates were plotted as a function of sample duration, mean response rate increased as a function of sample duration during the component in which pecks produced food following long samples, and decreased as a function of sample duration during the component in which pecks produced food following short sample durations. The point of subjective equality (PSE) is the point on the function where 50% of the responses are to the choice option corresponding to a long sample duration. This point reflects the sample duration that is perceptually in between the longest and shortest sample; that is, the sample duration that is neither short nor long. In this procedure, the neuropharmacological model of timing would predict overestimation of time, indicated by a leftward shift in the psychophysical function following exposure to amphetamine. Exposure to amphetamine dose dependently flattened the response functions but did not produce a systematic shift in the PSE. This result is indicative of a general disruption of timing.

The results of Odum et al. (2002) highlight some serious discrepancies in the timing literature. Although many experiments (e.g., Eckerman et al., 1987; Frederick & Allen, 1996; Maricq et al., 1981) have reported overestimation of time as a result of administration of dopamine agonists, many others have reported underestimation or generalized disruption of timing (e.g., Frederick & Allen; Knealing & Schaal, 2002; Odum et al.). The reasons for these discrepancies have yet to be resolved. Results from previous studies have suggested that the species and sex of the subject, and the route of administration of the drug cannot account for the discrepancies (Çevik, 2003; Odum, 2002; Odum et al.).

Chiang et al. (2000) helped to clarify this issue. They suggested that procedural differences might be at least partially responsible for the current discrepancies in the timing literature. To test this possibility they conducted two experiments in which they assessed the effects of amphetamine on behavior maintained by two different timing procedures. In their first experiment they arranged a free-operant psychophysical procedure (Stubbs, 1976). During this procedure rats distributed their responses between two levers during a 50-s trial. During the first half of the trial, responses on lever A were reinforced on a variable-interval (VI) 30-s schedule and responses on lever B had no consequence. A VI schedule arranges a reinforcer following the first response after a period of time that varies around some average (Ferster & Skinner, 1957). During the second half of the trial, responses on lever B were reinforced on a VI 30-s schedule and responses on lever A had no consequence. In the absence of amphetamine, response rates were high on lever A during the first half of the trial and decreased during the second half of the trial. Conversely, response rates on lever B were low during the first half of the trial and increased during the second half of the trial. Amphetamine increased low response rates and decreased high response rates. When the percentage of responses on lever B (%B) was plotted as a function of sample duration, the resulting psychophysical function indicated that, in the absence of amphetamine, the rats were discriminating the passage of time accurately. Amphetamine dose-dependently flattened the psychophysical function and shifted it slightly to the left, indicating overestimation of time.

In the second experiment, rats responded on an interval bisection task (Catania, 1970). Trials began with the illumination of a lamp for either 2 or 8 s. A response on

lever A was reinforced following a 2-s duration, and a response on lever B was reinforced following an 8-s duration. Sessions consisted of 120 trials. During the testing phase, 100 of the trials were standard, with the lamp being lit for either 2 or 8 s. During the remaining 20 trials the lamp was lit for a duration between 2 to 8 s. When %B responses were plotted as a function of stimulus duration, response functions during control conditions once again indicated that the rats were accurately estimating the passage of time. Amphetamine flattened the psychophysical function somewhat but did not shift it to the left. This result indicates a general disruption of timing.

The results of Chiang et al. (2000) confirm that amphetamine disrupts performance maintained by temporal discrimination procedures. The results of Experiment 1, however, could be interpreted as indicative of overestimation of time, while the results of Experiment 2 indicated a generalized disruption of timing. Chiang et al. cited additional evidence that the same pharmacological intervention can have different effects on timing when different timing tasks are used (e.g., Al-Ruwaitea, Al-Zahrani, Ho, Bradshaw, & Szabadi, 1997).

The free-operant psychophysical procedure used in Experiment 1 has traditionally been thought of as an immediate timing procedure (Killeen & Fetterman, 1988). In these types of procedures, the animal must regulate its behavior based on the passage of some temporal interval. The interval bisection task, however, has been classified as a retrospective timing task, in that the animal must make a different response depending on whether the presented sample duration was short or long. Based on the different results from these two experiments, Chiang et al. (2000)

concluded that different types of timing procedures might involve the use of different neural mechanisms. Specifically, the mechanisms underlying timing of some aspect of a subject's own behavior (immediate timing) may be different than the mechanisms involved when timing the duration of some experimenter-imposed event (retrospective timing). Thus, Chiang et al. concluded that the discrepancies in the timing literature may result partly from the fact that the effects of drugs on behavior maintained by timing procedures may differ depending on whether a subject is timing some aspect of its own behavior or some external event.

Timing of Subject-Produced Durations

Most studies of timing have been conducted using procedures that require animals to categorize the duration of an experimenter-imposed stimulus. Relatively little research has been conducted on the timing of subject-produced durations. This type of timing differs from timing of experimenter-imposed stimuli because the subject is required to temporally differentiate responding to produce a duration of some length, after which it is required to categorize the recently emitted duration.

Some research has been conducted on timing of subject-produced durations. For example, Zirix and Silberberg (1978) arranged a procedure in which pigeons emitted pecks to a blue center key. In Experiment 1 pecks resulted in a choice trial if the duration of the peck fell into one of three categories: 0 msec (no peck), 0-20 msec (short pecks), and 60-90, 110, or 180 msec (long pecks). The effective duration category was randomly chosen from trial to trial. After the effective peck was emitted, three different colored keys were lit, each color associated with a certain

category of peck durations. Pecks to the key that corresponded to the previous peck duration resulted in food. They found that all subjects were able to discriminate the prior peck duration. In Experiment 2 the center key was lit with the color indicating the correct response duration band at the beginning of the trial. Subjects were able to reliably produce and discriminate the peck duration.

In another experiment, Reynolds (1966) investigated the discrimination of duration. In his experiment, pigeons pecked a red key twice. The second peck turned the key blue. If the time between the first and second peck (IRT) was at least 18 s the schedule operating during blue was a VI schedule of food delivery. If the IRT was less than 18 s, the schedule in effect during blue was extinction. This contingency resulted in a differential-reinforcement-of-low-rate (DRL) schedule on the red center key. Reynolds found that the pigeons did not produce many IRTs of 18 s or more during the DRL schedule, indicating poor temporal control of the behavior by the contingency. The response rates during the second component, however, seemed to indicate that the pigeons were able to discriminate the duration of their IRTs. This discrimination was indicated by the fact that rates of pecking the blue key after IRTs greater than 18 s were higher than after IRTs less than 18 s. Although the results from this experiment suggest that the temporal behavior was not well controlled by the contingencies, an alternative explanation is possible. Rather than timing the duration of their own IRTs, the birds could have timed the duration of the red key, which was perfectly confounded with IRT duration. This explanation would account for why the birds were relatively unable to produce the required IRTs, yet could discriminate the IRT duration.

Shimp (1981) developed another procedure to test the discrimination of interresponse duration. He trained pigeons to make two pecks to a center key. He classified IRTs between 1.5 and 2 s as short, and IRTs between 4.5 and 7 s as long. To control for the confound in Reynolds' (1966) experiment (i.e., in which IRT duration was the same as key light duration), Shimp arranged a random-interval (RI) schedule on the center key. In an RI schedule, a reinforcer is delivered following the first peck after a period of time that varies randomly around some average (Millenson, 1963). Following the completion of the RI the computer selected which IRT class would be reinforced. The effective IRT class (short or long) was randomly chosen from trial to trial. During training, both classes of IRTs were reinforced, such that the birds produced IRT distributions with one large mode at around 1.5 s and another, smaller mode at around 4.5 s. To test discrimination of IRTs, Shimp periodically inserted symbolic matching-to-sample (SMTS) trials. After the chosen IRT was emitted, a retention interval was followed by the lighting of two side keys. The keys were lit different colors, each color corresponding to a class of IRT durations, either short or long. A peck to the color corresponding to the most recently emitted IRT resulted in food. Shimp found that pigeons were able to emit the required IRTs and categorize them correctly. Accuracy of discrimination decreased as a function of increasing retention interval. This decrease in accuracy with increasing retention intervals is consistent with data from other experiments on animal timing of experimenter-imposed stimuli (e.g., Leblanc & Soffie, 2001; Spetch & Wilkie, 1983).

Little research has been conducted on the effects of drugs on the discrimination of subject-produced durations. Chiang et al. (2000) suggested that effects of drugs

might differ for subject-produced and experimenter-imposed timing. Shimp's IRT discrimination procedure provides a way to examine the effects of drugs on this type of timing. This procedure also provides a way to assess the effect of drugs on the production of, as well as discrimination of, temporal durations.

Odum and Ward (2004) used a procedure based on the one described above to investigate the effects of morphine on the production and discrimination of IRTs. In their procedure pigeons made IRTs of different lengths and then categorized the duration of the recently emitted IRT. In the absence of morphine, pigeons produced a bimodal distribution of IRTs, with the modes close to the required duration categories. Pigeons also categorized the duration of the IRTs correctly at least 80% of the time. Morphine dose-dependently flattened the IRT distributions, indicating a general disruption in the temporal patterning of behavior. More importantly, morphine also affected accuracy for discrimination. Accuracy for discrimination of short durations was less affected than accuracy for discrimination of long durations. The pigeons chose short when the to-be-timed duration was long and chose short when the to-be-timed duration was short. This result could be interpreted to indicate underestimation of time. The results of this experiment are similar to those from other experiments in which pigeons timed the duration of an experimenter-imposed stimulus (e.g., Odum & Schaal, 2000).

Although the results of Odum and Ward (2004) do not support the conclusions of Chiang et al. (2002), caution must be used in interpreting their findings. Their experiment was not a direct comparison of the effects of morphine on the timing of experimenter-imposed and subject-produced stimuli. Rather, it assessed the effects of

morphine on only one type of timing (i.e., of subject-produced durations). To better assess the effects of drugs on both types of timing, it is necessary to conduct an experiment that provides a direct comparison of the effects of morphine on the timing of both subject-produced and experimenter-imposed stimuli.

The present experiment assessed the effects of morphine on the discrimination of subject-produced and experimenter-imposed stimuli. Although amphetamine has been commonly used to assess the effects of drugs on timing, it has been shown to drastically impair the production of relatively longer IRTs in other procedures (e.g., Sanger, Key, & Blackman, 1974). In the present procedure, pigeons make IRTs of different lengths: short and long. Therefore, it is likely that the administration of amphetamine would make it difficult for the pigeons to produce the requisite long IRTs. Morphine was chosen for the present experiment because Odum and Ward (2004) showed that although morphine disrupted the temporal patterning of behavior, pigeons were still able to produce longer IRTs.

STATEMENT OF THE PROBLEM

The study of the effects of drugs on timing has led to discrepant findings. Some experiments have found overestimation of time, while others have reported underestimation or generalized disruption of timing. Chiang et al. (2000) suggested that the discrepant results could be in part a result of different procedures used in different experiments. In two experiments, they showed that the procedure used can, in fact, influence the results. They suggested that drugs may have different effects on timing of subject-produced and experimenter-imposed durations. Recently, Odum and Ward (2004) assessed the effects of morphine on timing using a procedure that required pigeons to categorize the duration of their emitted IRTs. Their results were similar to those found when pigeons timed the duration of an experimenter-imposed stimulus.

There are two general types of procedures arranged in experiments that assess timing. One type requires the subject to time some aspect of its own behavior, while another type requires timing of some experimenter-imposed stimulus. Because of discrepancies in the reported results from experiments that use different timing tasks, it would be useful to create a procedure that allows a within-session assessment of both types of timing (i.e., subject-produced and experimenter-imposed). The current research arranged a multiple schedule composed of a subject-produced timing task and a yoked experimenter-imposed timing task. The experiment allowed for an assessment of the effects of morphine on the behavior associated with both types of timing tasks. Furthermore, this procedure allowed for this assessment to be conducted within the same subject within the same session.

METHOD

Design

This experiment used a small-*N* "single-subject" design in which each animal experiences all experimental conditions. The animal's behavior in one condition serves as the control or comparison for its behavior under other conditions (Sidman, 1960). Large quantities of data are gathered from a relatively small number of animals and conditions are run for extended periods of time. Multiple replications are performed, minimizing the number of animals used and intersubject variability. Judgments about stability of data are typically made by visual inspection and descriptive, rather than inferential, statistics.

Subjects

Three adult White Carneau pigeons served as subjects. Two other pigeons died during the course of the experiment. Data from these birds are not included. Pigeons were maintained at 80% (+/- 15g) of free-feeding weights by post session feeding as needed. The three pigeons had a previous experimental history with a variety of related procedures and had been exposed to morphine in previous experiments. The most recent administration of morphine was 2-3 years ago. Between sessions, pigeons were individually housed in a temperature-controlled colony under 12:12 hr light/dark cycle and had free access to water and digestive grit.

Apparatus

Four BRS/LVE sound-attenuating chambers were used. Chambers were constructed of painted metal with aluminum front panels. The chambers measured 35 cm across, 30.7 cm deep, and 35.8 cm high. Each front panel had three translucent plastic keys that could be lit from behind with green, white, red, amber, and blue light and required a force of at least 0.10 N to record a response. Keys were 2.6 cm in diameter and 24.6 cm from the floor. A lamp (28 V 1.1 W) mounted 4.4 cm above the center key served as a houselight. A rectangular opening 9 cm below the center key provided access to a solenoid-operated hopper filled with pelleted pigeon chow. During hopper presentations, the opening was lit with white light and the houselight and keylight were extinguished. White noise and chamber ventilation fans masked extraneous noise. Contingencies were programmed and data collected by a microcomputer located in an adjacent room using Med Associates® interfacing and software.

Procedure

No hopper or keypeck training was necessary for any of the birds. Experimental sessions occurred 7 days a week at approximately the same time. All birds had extensive history with an IRT-categorization procedure similar to that used and explained in detail in Odum and Ward (2004). This procedure constituted the subject-produced component. To allow time for drug absorption prior to selected sessions, all sessions began with a 10-min chamber blackout. Following the blackout, the houselight was lit and the center key was lit red to begin the session. The procedure

consisted of a multiple schedule in which there were subject-produced and experimenter-imposed components.

Subject-Produced Component

Sample production. In the first, or subject-produced component, pigeons categorized the duration of their IRTs. The procedure was based on one developed by Shimp (1981). Pigeons made pecks to a center key. The amount of time between pecks (IRT) was recorded. For the purposes of this experiment, IRTs between 2-3 s were classified as short and IRTs between 6-9 s were classified as long. An RI 20-s schedule was in effect on the center key. This schedule was programmed by arranging a choice trial with a probability of .0375 every 0.75 s. During the RI pecks to the center key provided response feed back via a .05-s extinction of the house and key light. When the RI timed out, the computer randomly selected whether a short or long IRT would result in a choice trial with the requirement that an equal number of trials follow short and long IRTs during each session. When the chosen IRT was produced, a choice trial began.

Choice trials. During choice trials, the center keylight was extinguished and the side keys were lit, one green and one white. The location of each color (left or right key) varied randomly from trial to trial. Pecks made to the key that corresponded to the previously emitted IRT resulted in a 3-s presentation of food. A peck to the other key resulted in a 3-s blackout. For bird P84, during a trial following a short IRT, a peck to the white side key resulted in food and a peck to the green side key resulted in a blackout. During a trial following a long IRT, a peck to the green key resulted in food and a peck to the white key resulted in a blackout. This color assignment was

reversed for birds P53 and P76. During each trial, the time it took for the RI to time out plus the time it took for an effective IRT to be made (obtained RI duration) were recorded for use in the second component. The duration of all IRTs that served as samples was also recorded for use in the second component. These durations were stored and used to equate the duration of the subject-produced and experimenter-imposed stimuli. Following eight choice trials, the second component began.

Experimenter-Imposed Component

Sample production. At the beginning of the second, or experimenter-imposed component, the computer randomly chose one of the eight obtained RI durations that had been stored from the first component. This duration constituted the intertrial interval (ITI). During the ITI, the houselight remained on and the keys were darkened. Following the ITI the center key was lit amber. This key served as a trial-ready stimulus to ensure that the bird was attending to the sample.

Following a peck to the amber center key, the computer randomly selected an IRT duration that had been stored from the first component. The key was lit blue for the duration of the selected IRT, after which it was darkened. This duration constituted the sample. The duration of the sample corresponded to the durations in the first component, with durations of 2-3 s classified as short and durations of 6-9 s classified as long.

Choice trials. Following the termination of the sample, the side keys were lit, one green and one white. A peck to the key color that corresponded to the duration of the sample resulted in food. An incorrect choice resulted in a 3-s blackout. The colors corresponding to short and long durations for each pigeon were as in the first

component. Following eight trials, the program switched back to the first component. Each component was presented for three blocks of eight trials. Daily sessions ended after 48 trials.

Correction Procedure

Early during training, if matching accuracy was low because of a pronounced color or side bias, a correction procedure was instated (cf. Shimp, 1981). In this procedure, a peck to the incorrect key during a choice trial was followed by the darkening of the side keys for 3 s. The side keys were then relit with the same colors in the same positions. This process continued until a correct response produced food and ended the choice trial.

Morphine Tests

Drug testing began for individual pigeons when the IRT distributions and matching accuracy were stable and asymptotic as judged by visual inspection. The criterion for IRT discrimination was 10 consecutive sessions in which accuracy was at least 80% for both long and short categories without any evident trend or unusual variability in the data.

Morphine sulfate (Sigma) was dissolved in 0.9% saline and administered in a volume of 1.0 ml/kg of the 80% free-feeding body weight. Morphine and vehicle were administered via intramuscular injections into the breast before the pigeon was placed in the experimental chamber. In order to accustom the birds to the injection procedure, they were given a preliminary injection of saline. Results of these injections were excluded from the analysis. Sessions preceding a morphine or saline injection were designated as control sessions.

Following the preliminary injections, morphine and vehicle were given in the following order: 1.0 mg/kg, 3.0 mg/kg, 0.56 mg/kg, 5.6 mg/kg, and saline. This range of doses has previously been shown to allow a thorough examination of the effects of morphine on the behavior maintained by tasks of this type. Tests were separated by at least three consecutive baseline sessions not preceded by an injection. The effects of all doses and saline were examined before any dose was repeated. The effects of saline and each drug dose were determined at least three and a maximum of four times.

RESULTS

The next three figures show the effects of morphine on the temporal differentiation of behavior during the subject-produced component. Figure 2 shows the mean relative frequency of IRTs as a function of IRT duration for each pigeon during control sessions (top row) and across doses of morphine (lower rows). The control distributions show a burst of short IRTs in the 0-0.25-s bin. Aside from this burst, the IRT distributions were roughly bimodal for all pigeons, with a large mode near the 2-3 s (short) category and a much smaller mode near the 6-9 s (long) category. These results indicate that the contingencies effectively shaped IRT production. Morphine (lower rows) increased the proportion of IRTs that were less than 1 s for two of the three birds. This effect was most pronounced for P76. Aside from this increase, morphine had relatively little effect on the distributions for P76 and P53. Morphine dose-dependently shifted the IRT distribution to the left for P84.

To further assess the effects of morphine on the production of IRTs during the subject-produced component, an IRTs per Opportunity analysis (IRTs/Op; Anger, 1956) was conducted. As seen in Figure 2 pigeons emitted many more IRTs in the short category than in the long category. Short IRTs take less time to emit than long IRTs, so for example, two 3-s IRTs could be emitted in the time that it takes to emit one 6-s IRT. To directly compare the relative frequency of short and long IRTs becomes problematic in this case because there are a greater number of opportunities to emit short IRTs. An IRTs/Op analysis gives the probability of making an IRT of a particular duration conditional upon the number of opportunities to make the IRT, thereby giving another estimation of the frequency of both types of IRTs. To calculate

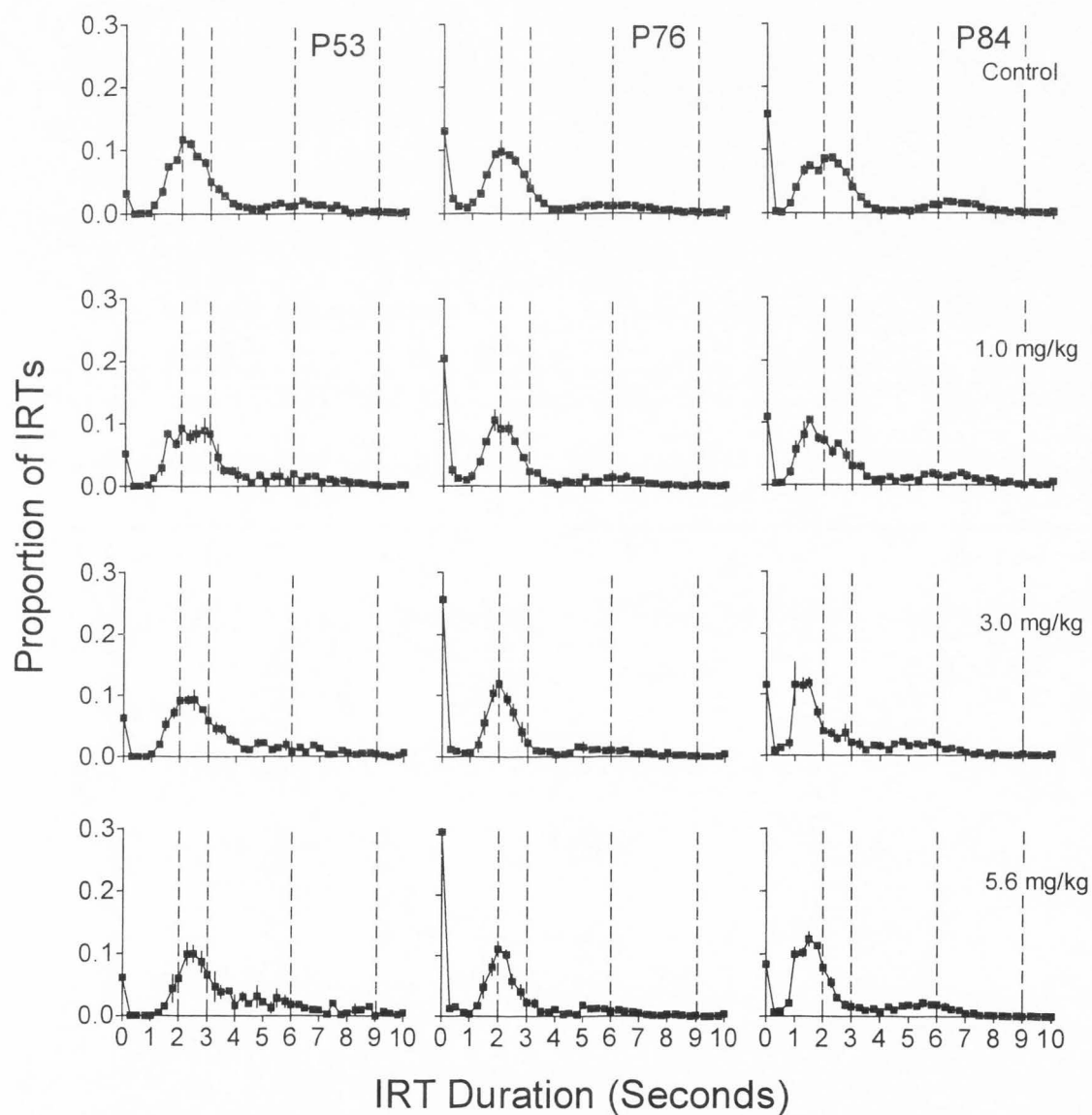


Figure 2. Mean relative frequencies of interresponse times as a function of interresponse time duration in 0.25-s bins during control sessions (top row) and across doses of morphine (lower rows) for each pigeon. Dotted vertical lines indicate the boundaries of the short and long categories. Vertical bars represent one standard deviation above and below the mean. In some cases the variability around a point is obscured by the point.

this probability, the number of IRTs in each 0.25-s class was divided by the number of IRTs in that class plus the number of all longer IRTs.

Figure 3 shows the mean IRTs/Op as a function of IRT duration during control sessions and across doses of morphine for all pigeons during the subject-produced component. The IRTs/Op distributions have one clear mode in the bounds of the short category and a second, less clear mode in the bounds of the long category. The number of IRTs/Op in the long category tended to increase and decrease across the category, and this mode was more variable than the mode in the short category. The overall frequency of IRTs/Op in the short and long category were more similar than in Figure 2. These results show that given the opportunity to emit a short or long IRT, the number of short and long IRTs emitted was similar. Morphine tended to flatten the mode corresponding to the long category of IRTs somewhat for all birds. Also, as indicated in Figure 2, morphine shifted the distribution to the left for P84. The average effect of morphine on the IRTs/Op across birds is shown in Figure 4. This figure shows that, across birds, the overall effect of morphine was to flatten the IRTs/Op distributions somewhat. This effect was particularly apparent for the long category of IRTs. The shape and location of the modes was not changed systematically as a function of morphine dose.

Figure 5 shows the effects of morphine on temporal discrimination during both the subject-produced and experimenter-imposed components. The left panels show accuracy for categorizing the short and long IRTs in the subject-produced component. During control sessions, accuracy for categorization of both short and long IRTs was above 85% for all pigeons. Saline had no systematic effect on accuracy for

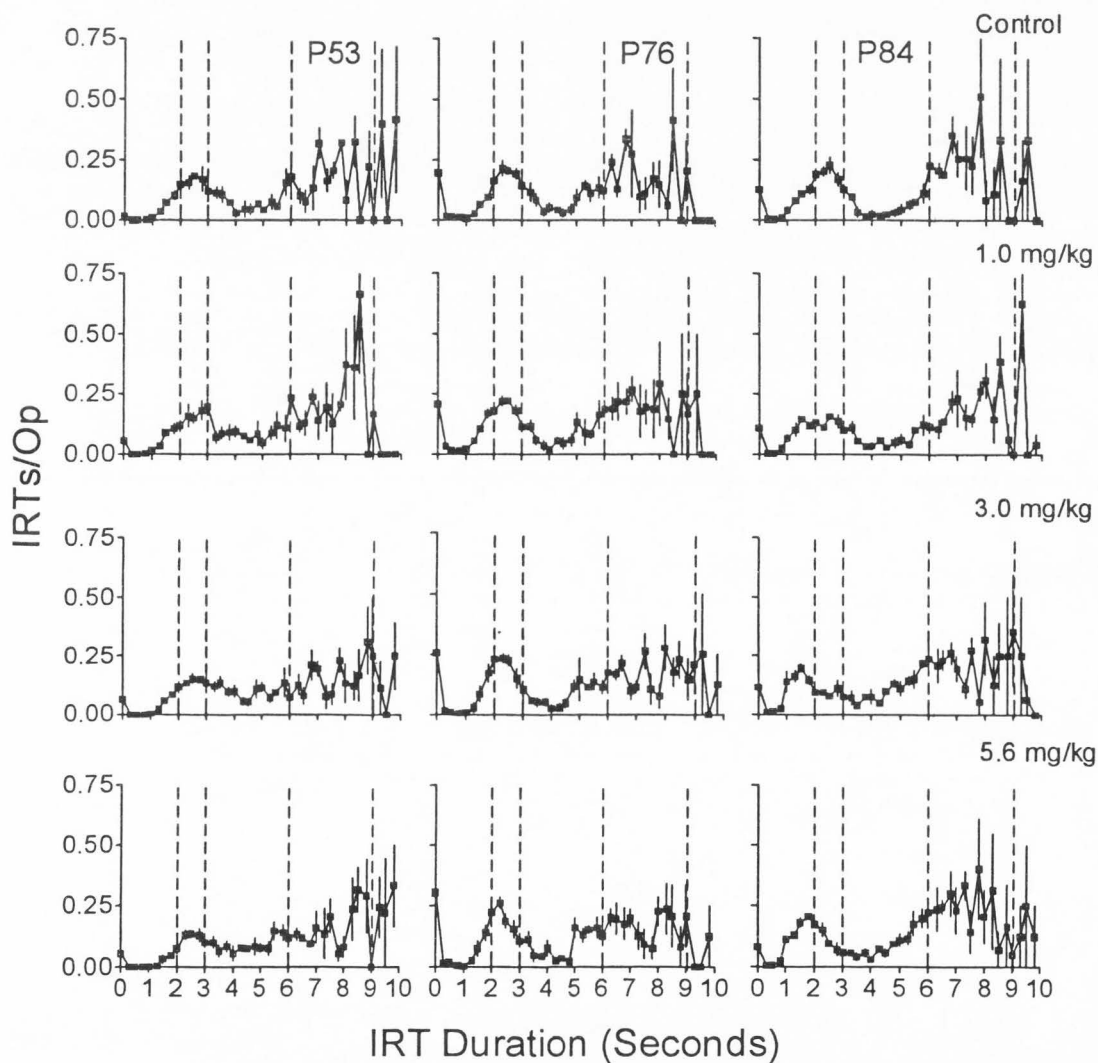


Figure 3. Mean IRTs per opportunity as a function of IRT duration for each pigeon during control sessions (top row) and across doses of morphine (lower rows). Vertical bars represent one standard deviation above and below the mean. Other details as in Figure 2.

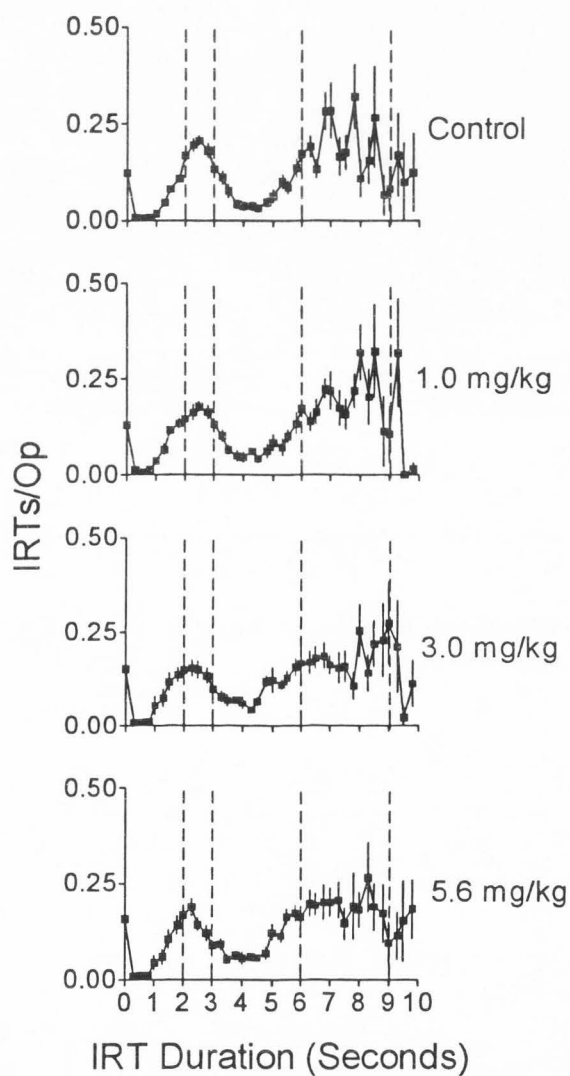


Figure 4. Mean IRTs per opportunity as a function of IRT duration during control sessions (top row) and across doses of morphine (lower rows). Data shown are averaged across pigeons. Vertical bars represent one standard error above and below the mean. Other details as in Figure 3.

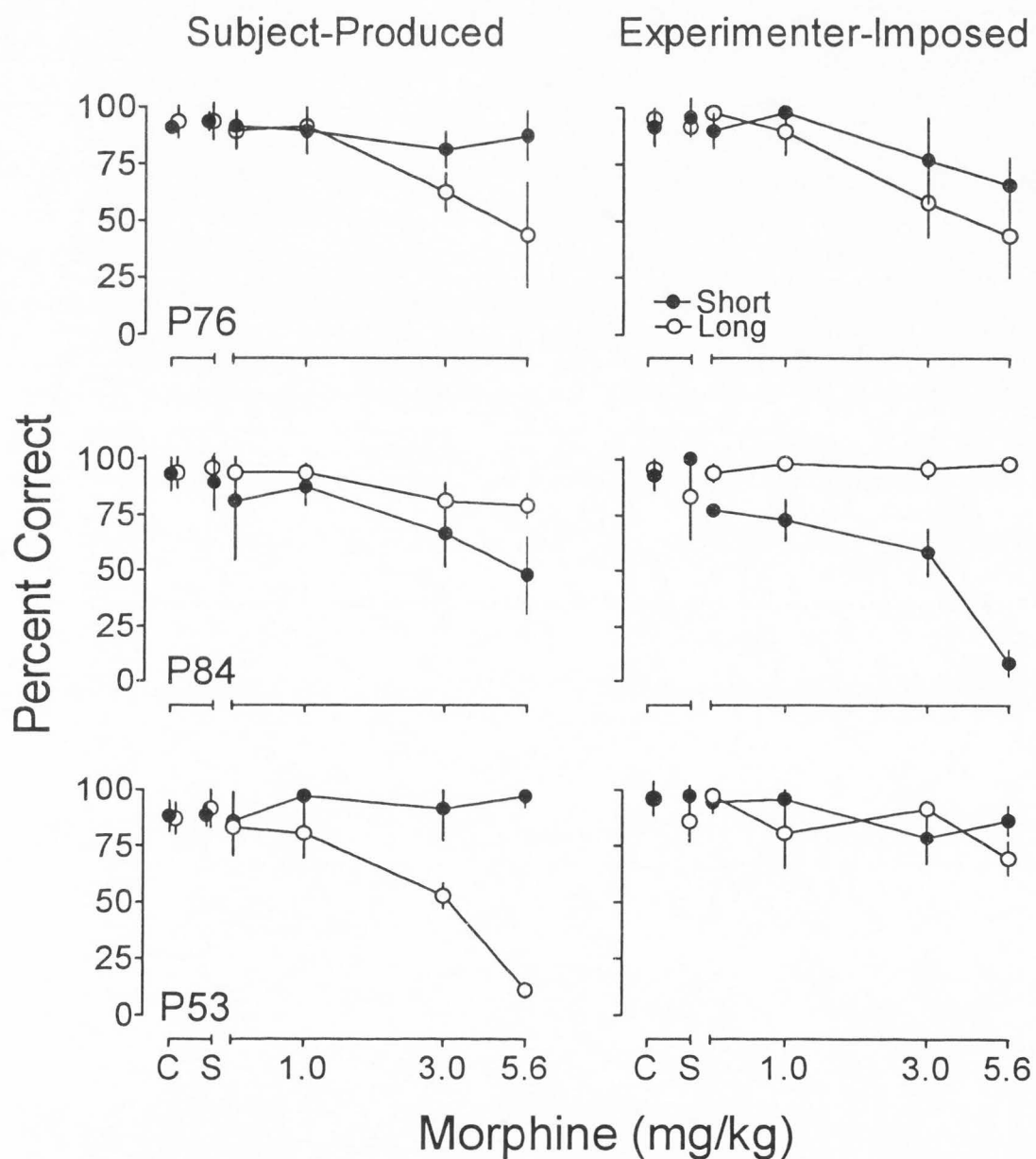


Figure 5. Percent correct categorization for short and long samples for each pigeon during the subject-produced (left column) and experimenter-imposed (right column) components. Vertical bars represent one standard deviation above and below the mean. Unconnected points show means for all control (C) and saline (S) sessions. Lines connect points showing mean percent correct across doses of morphine. Open circles represent percent correct for sample durations in the long category and closed circles represent percent correct for sample durations in the short category.

categorization of either IRT duration. For two of the three birds (P76 and P53) morphine dose-dependently decreased accuracy for categorization of long IRTs, while accuracy for categorization of short IRTs remained relatively unaffected. For P84, the opposite effect was observed. For this pigeon, morphine decreased accuracy for categorization of short IRTs more than for categorization of long IRTs.

The right panels of Figure 5 show the effects of morphine on discrimination of sample durations in the experimenter-imposed component. Accuracy for discrimination of short and long temporal samples was above 85% during control sessions. Saline decreased accuracy for discrimination of long samples slightly for all birds. Morphine had no systematic effect on accuracy of categorization across birds. For P76, morphine dose-dependently decreased accuracy for discrimination of both short and long temporal samples. Accuracy for discrimination of long samples was more affected than accuracy for discrimination of short samples. For P84, morphine dose-dependently decreased accuracy for discrimination of short samples, while accuracy for discrimination of long samples was relatively unaffected. For P53, the overall effect of morphine was a decrease in accuracy of categorization for both short and long temporal samples, although the decrease was not systematic for either short or long samples. In summary, morphine disrupted accuracy for categorization of both short and long samples. However, the disruption was not systematic across the three pigeons.

All analyses to this point have assumed choice behavior in the experimenter-imposed component was under the functional control of the presented sample durations. Given the birds' previous history of making and categorizing their IRTs on

the center key, however, it is possible that the birds continued this behavior during the experimenter-imposed component. Observation of the birds during experimental sessions showed that some did in fact peck the center key during sample presentations. To examine the possibility that choice behavior was under the functional control of the most recently emitted IRT on the center key, the next two figures show the proportion of responses to the long key color as a function of IRT duration on the sample key during short (Figure 6) and long (Figure 7) sample trials during control sessions (top row) and across doses of morphine (lower rows). Data are shown only for P76 and P84, as P53 made a minimal number of IRTs on the center key during sample presentations across all conditions of the experiment. The mean number of IRTs on the center key during sample presentations for this bird per session was 0.067 and 0.22 for control sessions, and across all drug sessions, respectively. In these figures, control by the preceding sample duration would be indicated by functions that do not increase or decrease systematically as a function of IRT duration. Control by the most recently emitted IRT duration would be indicated by functions that increase as a function of IRT duration.

Figure 6 shows that during short sample presentations, under control conditions, in general P76 made few long choices following IRTs of any duration, while P84 showed an increase in the proportion of choices to the long key color as a function of increasing IRT duration. Across doses of morphine, proportion of long choices did not increase as a function of increasing IRT duration for P76, except at IRT durations of 2 s at 3.0 and 5.6 mg/kg. For P84, the proportion of long choices increased as a function of increasing IRT duration. At 5.6 mg/kg, the proportion of long choices

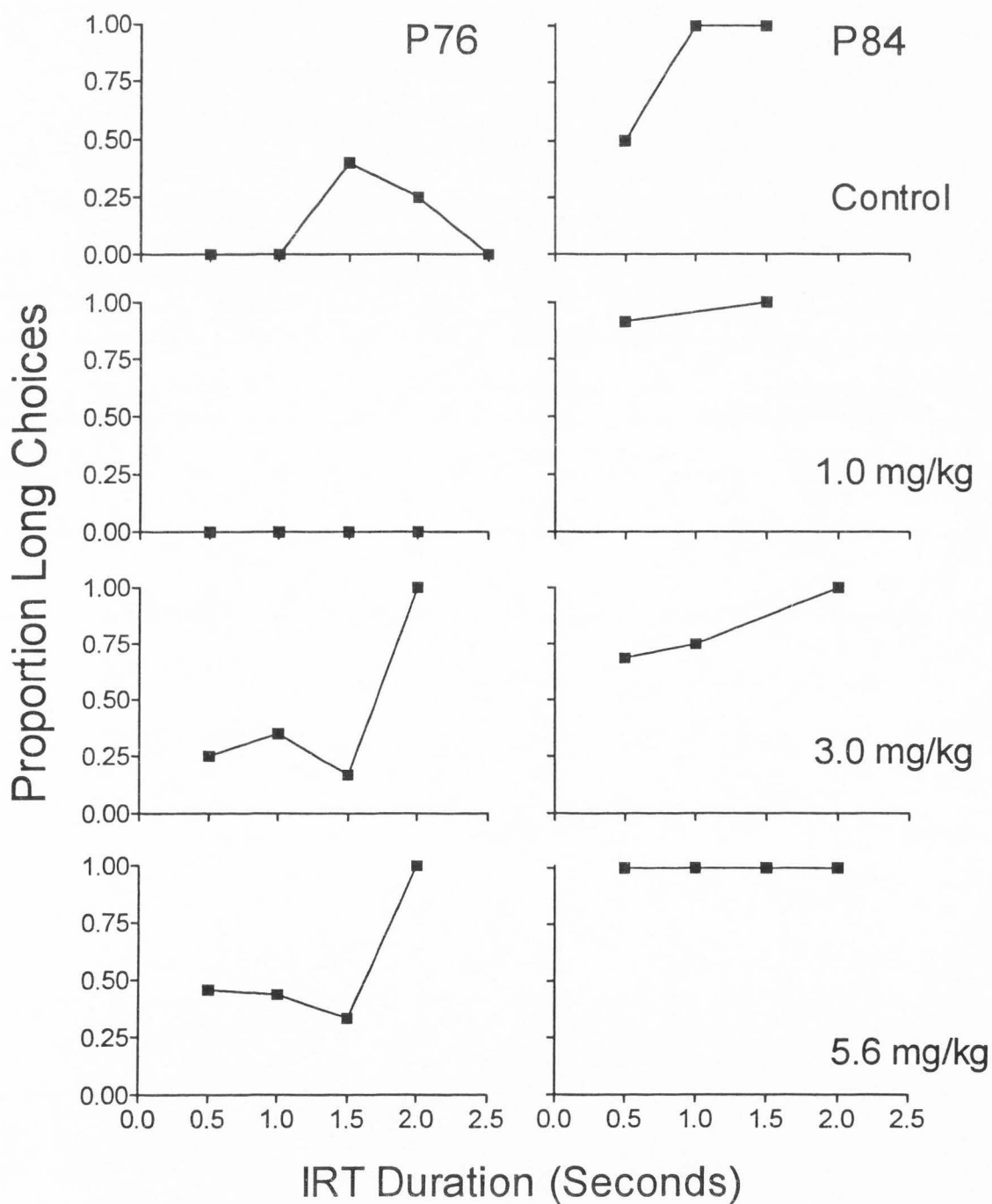


Figure 6. Proportion of choices to the long key color as a function of IRT duration for P76 and P84 during control (top row) and morphine (lower rows) sessions during the experimenter-imposed component. Data shown are for trials during which a short (2-3 s) sample was presented.

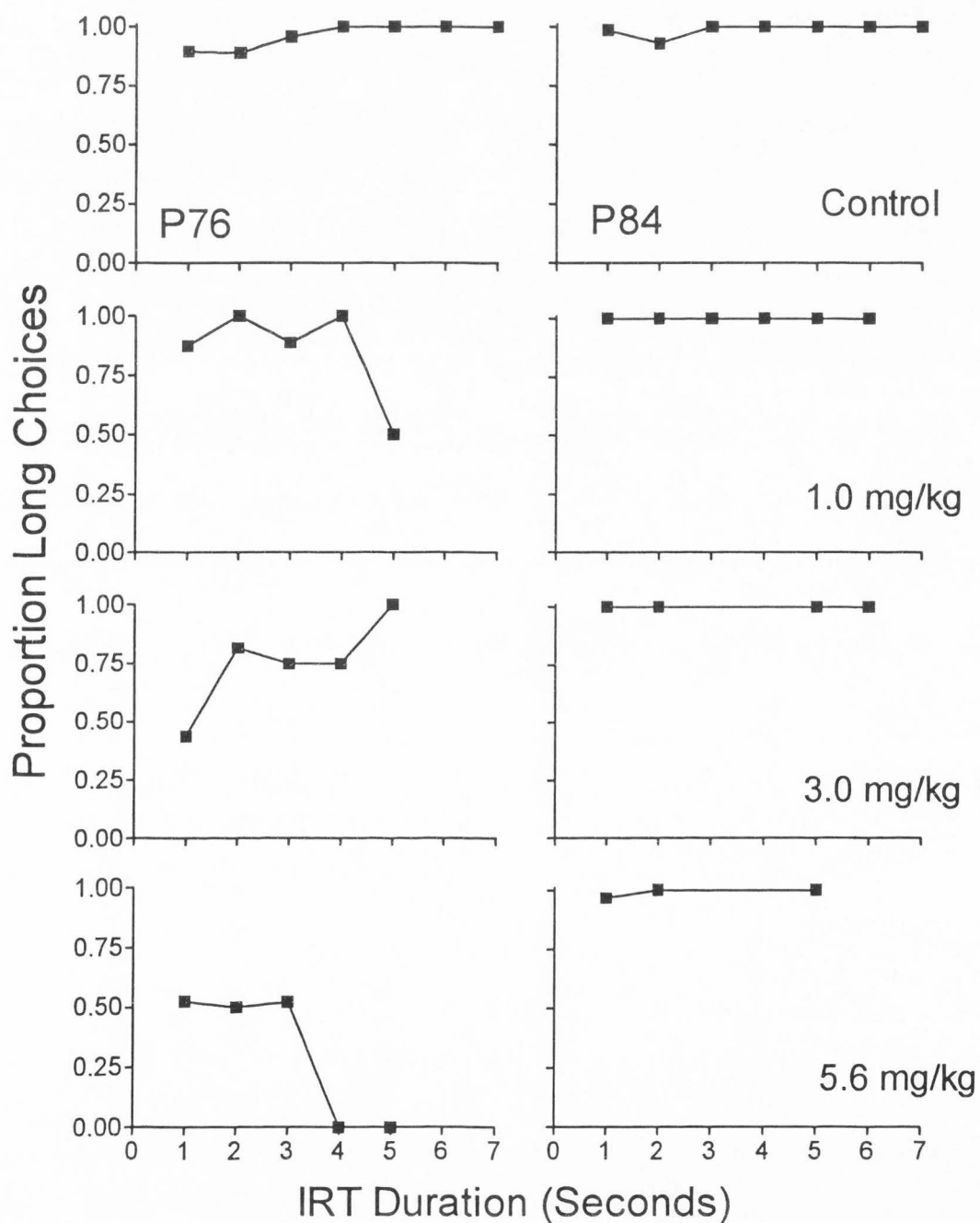


Figure 7. Proportion of choices to the long key color as a function of IRT duration for P76 and P84 during control (top row) and morphine (lower rows) sessions during the experimenter-imposed component. Data shown are for trials during which a long (6-9 s) sample was presented.

following an IRT of any duration was 1.0. These data show that for P76, most control over choice behavior was by the preceding sample duration, although there was some increasing control by the longest IRT duration at higher doses of morphine. For P84, the proportion of long choices was relatively high, even under control conditions. Morphine dose-dependently increased the proportion of long choices following longer IRT durations.

Figure 7 shows that during control conditions during long sample trials, the proportion of long choices was high following IRTs of all durations for both birds. For P76, there was no consistent effect of morphine on the proportion of long choices as a function of IRT duration. The proportion of long choices increased at some IRT durations and decreased at others. For P84, the proportion of long choices following IRTs of all durations remained near 1.0 across all doses of morphine.

DISCUSSION

The baseline performance during the subject-produced component replicates that obtained by Shimp (1981, 1983) and more recently by Odum and Ward (2004). The IRT distributions were roughly bimodal, with one mode at the beginning of the short category (2-3 s) and a second smaller mode at the beginning of the long category (6-9 s). Further analysis of the IRT distributions showed that, under control conditions, given the opportunity to make a short or long IRT, the relative frequency of short and long IRTs was similar (IRTs/Op; Figure 3). During choice trials, accuracy for categorization of short and long samples during the subject-produced and experimenter-imposed components was above 85% for all subjects, with no systematic differences in categorization for the short or long samples.

Morphine had minimal effects on the temporal patterning of behavior during the subject-produced component. The average effect of morphine was to flatten the IRT distributions somewhat, although this effect was notably small. For two of the three birds during the subject-produced component, accuracy for categorization of long IRTs was decreased more than accuracy for categorization of short IRTs. For P84, the opposite effect was observed. During the experimenter-imposed component, morphine had no systematic effect on accuracy of categorization for either short or long samples across birds.

The effects of morphine on the temporal differentiation of behavior (i.e., IRT production) in the subject-produced component were somewhat different than those reported by Odum and Ward (2004). In their study, morphine produced a dose-dependent flattening of the IRT distributions, while in the present study, morphine

produced a general flattening of the distributions for two of the birds, though not in a dose-dependent manner. For the other bird, morphine shifted the distribution to the left. The reason for the different results is difficult to say. One possibility is the subjects' extensive previous experience with the procedure may have resulted in IRT production being more resistant to disruption by morphine than in the previous experiment. Although the general effect of morphine as evidenced by Figures 2 and 3 was to flatten the distributions somewhat, the magnitude of the results was less than that reported by Odum and Ward.

One obvious difference in the present procedure and that used by Odum and Ward (2004) was the use of a multiple schedule that employed two different types of timing procedures. This arrangement has not been used previously. Perhaps some aspect of the multiple schedule procedure employed in the present experiment contributed to the less apparent effects of morphine observed on IRT production.

The effect of morphine on the categorization of the short and long IRTs obtained in the subject-produced component replicates that found by Odum and Ward (2004). Morphine selectively disrupted categorization of long IRTs for two of three birds. This selective disruption could be interpreted as underestimation of the duration of the sample IRTs. Although the results obtained from P84 were clearly opposite in effect from those obtained from the other two birds, it may be of interest to note that this pigeon displayed the same opposite result in Condition 2 of Odum and Ward.

The results from this component further highlight the discrepancies in the literature on the effects of drugs on behavior maintained by temporal discrimination procedures. Furthermore, these results do not support the conclusions of Chiang et al.

(2000). They concluded that the effects of drugs on behavior maintained by temporal-discrimination procedures might differ depending on whether the subject is discriminating the duration of some aspect of its own behavior, or some experimenter-imposed stimulus. Specifically, Chiang et al. suggested that the effect of drugs on discrimination of subject-produced stimuli might result in overestimation of time. The results obtained from the subject-produced component in the present experiment are similar to those obtained by Odum and Schaal (2000) when subjects categorized the duration of an experimenter-imposed stimulus. They found a generalized disruption of temporal discrimination for both short and long samples, and results that could be interpreted as underestimation of time at the largest dose. The results from this component in general indicated a dose-dependent underestimation of time, and suggest that the effects of morphine may be similar on the discrimination of both subject-produced and experimenter-imposed stimuli.

The lack of a systematic effect of morphine on discrimination of samples in the experimenter-imposed component is difficult to account for. The results from numerous experiments have unequivocally shown clear effects of several types of drugs on behavior maintained by temporal-discrimination procedures similar to that used in the experimenter-imposed component in the current experiment. Although many experiments have assessed the discrimination of temporal experimenter-imposed stimuli, none to date have assessed them in a multiple schedule situation like that used in the current experiment. The prior results suggest that perhaps some aspect of the present multiple-schedule procedure contributed to the unsystematic effects

obtained in the experimenter-imposed component. There are several possible procedural contributions, and each will be discussed in turn.

The first possibility is that during the experimenter-imposed component, rather than categorizing the duration of the sample, the pigeons were categorizing the duration of their most recently emitted IRT on the center key. In the subject-produced component, the pigeons learned to temporally differentiate their pecks to produce two different categories of IRT durations. Furthermore, all pigeons received extensive history on this IRT categorization procedure prior to their first exposure to the experimenter-imposed component. Given this learning history, it is possible that when the center key was illuminated for the duration of the sample during the experimenter-imposed component, the pigeons continued emitting relatively shorter and longer IRTs on the center key. Observation of the birds during the experimenter-imposed component showed that some did indeed peck the center key during some sample presentations. During choice trials, the pigeons may then have responded to the key color that corresponded to their most recently emitted IRT duration, rather than categorizing the duration of the presented sample.

Although this explanation may seem plausible, several factors render it less compelling. First, the sample durations during the experimenter-imposed component were yoked to the IRT durations from the subject-produced component. Although some of the birds did peck the center key during sample presentations, the probability of emitting a short or long IRT (2-3 s for short and 6-9 s for long), given a short or long sample duration would be extremely low. This lack of predictability would make

it extremely difficult for the pigeons to be able to differentiate their responding in such a way as to produce a short or long IRT during any one sample.

Second, the results presented in Figures 6 and 7 show that for P84, during short sample trials, there was some influence of the preceding IRT duration under control conditions. During long sample trials, however, there appeared to be no influence of the preceding IRT duration on the proportion of long choices. During both short and long sample trials, the proportion of long choices was affected little by morphine and remained high during all doses. These results show that for P84 the proportion of long choices was not affected by morphine administration. Instead, this bird seemed to have a bias for the key color associated with long samples. For P76, morphine had no systematic effect on the proportion of long choices following any IRT duration. These results show that the pigeons were not basing their choice responses on the absolute (2-3 s for short and 6-9 s for long) or relative duration of the most recently emitted IRT. Furthermore, the effects of morphine on categorization of samples during the experimenter-imposed component were unsystematic for P53, and this pigeon emitted very few IRTs on the center key during sample presentations across all conditions. Taken together, these results suggest that the unsystematic effects observed in the experimenter-imposed component cannot be explained by appealing strictly to an IRT categorization account.

Another possible explanation for the unsystematic results in the experimenter-imposed component has to do with the length of the intertrial interval (ITI). During the subject-produced component, an RI-20 s schedule was in effect on the center key. Once the interval timed out, the next IRT that matched the chosen IRT category

resulted in a choice trial. Inspection of the IRT distributions shows that the relative frequency of IRTs in the short category was more than twice as great as the relative frequency of IRTs in the long category. On average then, the time it took for the RI to elapse plus the time until a chosen IRT was emitted would have been shorter for trials following a short IRT than for trials following a long IRT. Odum and Ward (2004) showed that while most choice behavior in this procedure was under the functional control of the preceding IRT duration, there was some influence of the preceding RI duration as well.

In the experimenter-imposed component, however, the ITI was yoked to a randomly chosen obtained RI duration from the first component. Therefore, unlike during the subject-produced component, the duration of the ITI had no relation to the sample duration. It is possible that whatever predictive ability the duration of the RI had in the subject-produced component was disrupted in the experimenter-imposed component due to the breaking up of the relation between the ITI and the sample duration. Furthermore, it is possible that once drugs were administered, functional control of the choice behavior shifted from the sample duration to the duration of the preceding ITI. This shift in control would be indicated by an increasing proportion of choices to the key color corresponding to a long sample duration as a function of increasing ITI. Unfortunately, due to a programming oversight, these data were not collected.

The results from the experimenter-imposed component could be due to several procedural interactions with the effects of morphine. One characterization of this interaction focuses on the discriminability between components of the multiple

schedule. Aside from the effects of morphine on temporal perception, morphine could have disrupted overall stimulus control. As dose increased, discrimination between components could have become more difficult. Adding to the plausibility of this explanation is the fact that the colors on the side keys during choice trials remained the same across components (green and white). Being exposed to the same key colors during choice trials may have contributed to lack of discriminability between components, or may have reinstated an IRT categorization strategy. Due to the yoking aspect of the procedure, the subject-produced component was always presented first in each daily experimental session. Because of this presentation order, the pigeons choice behavior was under the control of the preceding IRT when exposed to the first experimenter-imposed component, and this control by the preceding IRT may have been perpetuated by the presence of the same key colors during choice trials. The data presented in Figure 8 support this interpretation. Figure 8 shows the mean number of experimenter-imposed trials on which an IRT was made on the center key during sample presentations. Data shown are for P76 and P84 during control and saline sessions and across doses of morphine.

During control sessions for both birds, the number of trials with an IRT on the center key was about 6. Saline decreased the number of trials with an IRT slightly for both birds. Morphine dose-dependently increased the number of trials with an IRT on the center key during sample presentations for both birds. In fact, the number of trials with an IRT increased from about .25 of the total number of experimenter-imposed trials under control conditions, to nearly .75 of the total number at the highest dose of morphine. These results show that the birds made more IRTs in sessions following

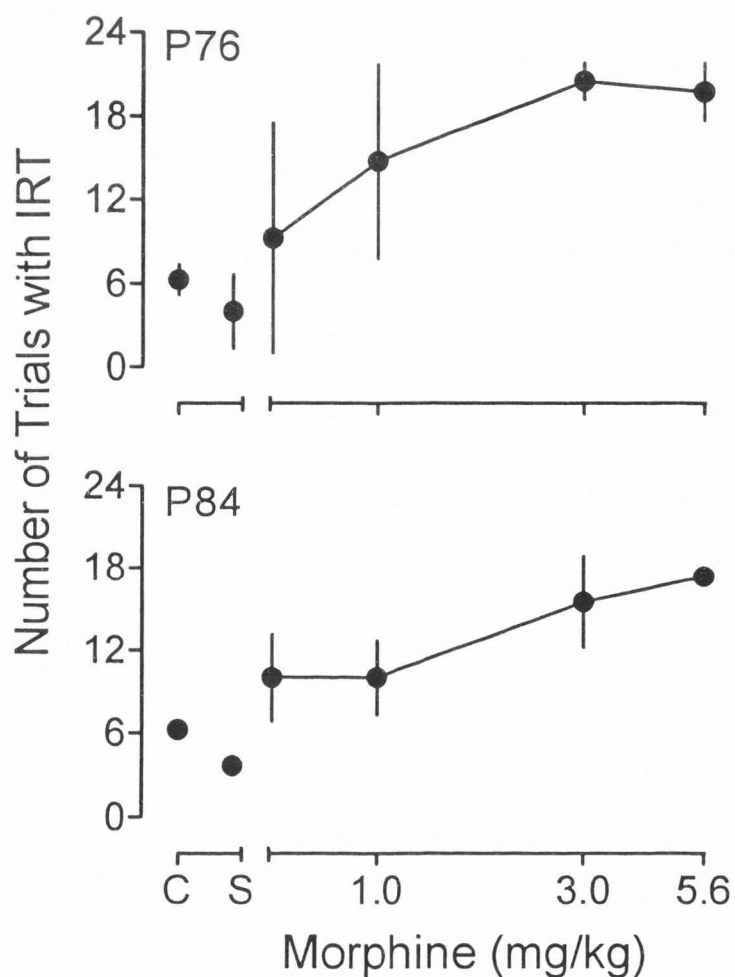


Figure 8. Mean number of trials on which an IRT was made on the center key during sample presentations during the experimenter-imposed component. Data shown are for P76 and P84. Unconnected points show the means for all control and saline sessions. Lines connect points showing means across higher doses of morphine. Vertical bars represent one standard deviation above and below the mean.

morphine administration than under control conditions. One could interpret these results as evidence of a morphine-induced loss of discriminability between components. In other words, following higher doses of morphine, it became increasingly difficult for the pigeons to discriminate which component they were in, and so they began emitting IRTs on the center key during the experimenter-imposed component.

Although the present analyses rule out an explanation of the results based solely on control of choice behavior in the experimenter-imposed component by the most recently emitted IRT, it is possible that a strategy of this type contributed to the unsystematic results. As discussed above, the probability of pigeons temporally differentiating pecks to the center key during sample presentations in such a way as to emit a short or long IRT before the sample presentation terminated was extremely low. Because of this probability, there would be some number of trials in which short samples were presented during which pigeons did not make an IRT. In addition, there would be some presumably long sample duration trials during which pigeons made several IRTs. If choice behavior in the experimenter-imposed component was under the functional control of the preceding IRT, the time between the last completed IRT and the termination of the sample could be characterized as a variable delay between the IRT sample and the comparison choices. Delays between the offset of a sample stimulus and the onset of the comparison stimuli degrade accuracy. Choice behavior may have been under the control of the preceding IRT, but due to the delay between the sample IRT and the comparison stimuli, choice responses were not accurate. In addition, pigeons could have been timing the current IRT when the temporal sample

terminated. Therefore, the unsystematic effects observed in this component could have resulted from choice behavior based on the most recently emitted IRT on the center key, coupled with guessing on trials in which the most recently emitted IRT could not be discriminated.

Another possibility is that morphine produced a bias for one particular choice key color during both components. The effects of morphine on accuracy of discrimination in both the subject-produced and experimenter-imposed components were similar for P76 and P84. For both pigeons, the administration of morphine decreased accuracy for one particular category of sample durations, long for P76 and short for P84. In addition, the key colors associated with short and long samples were the same across components. These results are consistent with a drug-induced bias for a certain key color. Unfortunately, both birds had different counterbalanced color assignments. Therefore it is not possible to separate distortions in temporal perception from bias for the key color associated with either the short or long sample. The differing results across components for P53, however, do not appear to be reconcilable by this account.

The results from the subject-produced component of the present experiment are in accord with the results of Odum and Ward (2004) in suggesting that the effects of morphine on the discrimination of subject-produced durations may be similar to that observed when subjects classify the duration of experimenter-imposed events. The lack of a systematic effect of morphine on categorization of samples in the experimenter-imposed component of the current experiment could be due to several procedural interactions with the effects of morphine. In this case, although differences

in accuracy for categorization of temporal stimuli were apparent, the lack of a systematic effect across birds did not facilitate a direct comparison of the effects of morphine on the discrimination of subject-produced and experimenter-imposed durations in this procedure.

In conclusion, several procedural modifications could help in obtaining a clear effect of morphine with the current procedure. For example, changing the key colors corresponding to short and long sample durations across components would help to control for any bias that was associated with any particular key color across components. In addition, if in fact morphine decreased discriminability across components, changing the key colors would make the two components more discriminable than they were in the current experiment. To assess the effect of the ITI on choice responses during the experimenter-imposed component, each respective ITI could be presented with the IRT sample it preceded. In this way, the degree of control by the preceding ITI could be more directly assessed, and we could detect increasing or decreasing control by the ITI as a function of morphine. Finally, multiple-schedule procedures of this sort may be too complicated for a clear effect to be established across components. Devising different types of procedures may be necessary to clearly examine the effects of drugs on discrimination of subject-produced and experimenter-imposed stimuli and lead to a better understanding of the neuropharmacological basis of timing.

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